Inter-tidal Zonation at Rangitoto Island, New Zealand. (Studies in Inter-tidal Zonation 4.)[1]

J. A. Carnahan[2]

INTRODUCTION

This study was undertaken to elucidate, if possible, the causative agents determining the distribution of inter-tidal plants and animals on the shores of Rangitoto Island. The work comprised an attempt to classify the inter-tidal communities, followed by an examination of tidal and other environmental factors.

I wish to thank Professor V. J. Chapman for his advice and criticism. My thanks are also due to Miss R. F. de Berg, Mr. V. W. Lindauer, Miss L. B. Moore, and Mr. J. E. Morton for assistance with identifications; to Mr. P. Carnahan for help with the instrument levelling; and to Mr. C. Harvey for preparing the graphs for reproduction. Finally, the work on Rangitoto was facilitated by the cooperation given by the Naval Department and by the staff at Rangitoto Naval Base.

DESCRIPTION OF LOCALITY

Rangitoto Island is situated in the southwest corner of the Hauraki Gulf, New Zealand, off the entrance to Auckland Harbour (Fig. 1). It is a roughly circular island, with a diameter of 3 miles. The western and southern coasts are about 3 miles from the mainland, while the adjoining island of Motutapu protects its eastern shores. Only the northern coast is exposed, but even this faces a gulf, not the open sea.

Rangitoto is a volcano which has been active in recent times. The greater part of the island consists of flow basalt and exhibits the characteristic low conical shape of such volcanoes. This portion is probably more or less contemporaneous with the Pleistocene basalt volcanoes which are of frequent occurrence in the Auckland metropolitan area. The final cinder cone within the original crater may have ceased activity within historic times.

The principal substratum is the basic lava which comprises the island volcano. Upon sheltered shores, this occurs as solid flows or as broken scoria (Fig. 2). On fairly exposed shores, the flows are somewhat broken and the scoria is waterwashed. On the more exposed northern coasts, the heavy surf raised by northeast winds has produced cliffing and boulder beaches.

Mud occurs as harbour silt beyond the termination of flows and scorias. It also appears wherever it is possible for sedimentation to take place. It is conspicuous in protected bays and inlets and on scoria shores. Minor, localised substrata are developed from "natural brick" (sedimentary material baked by contact with hot lava), sand, and shell.

TERMINOLOGY

The writer follows Chapman (1946) and Beveridge and Chapman (1950) in applying terrestrial plant ecological terminology to inter-tidal communities of plants and animals. This is based on the assumption of the cli-

[1]This paper contains the substance of a thesis presented at Auckland University College for the degree of M.Sc., 1948.

[2]Junior Lecturer, Department of Botany, Massey Agricultural College, Palmerston North, New Zealand.
Manuscript received August 2, 1949.

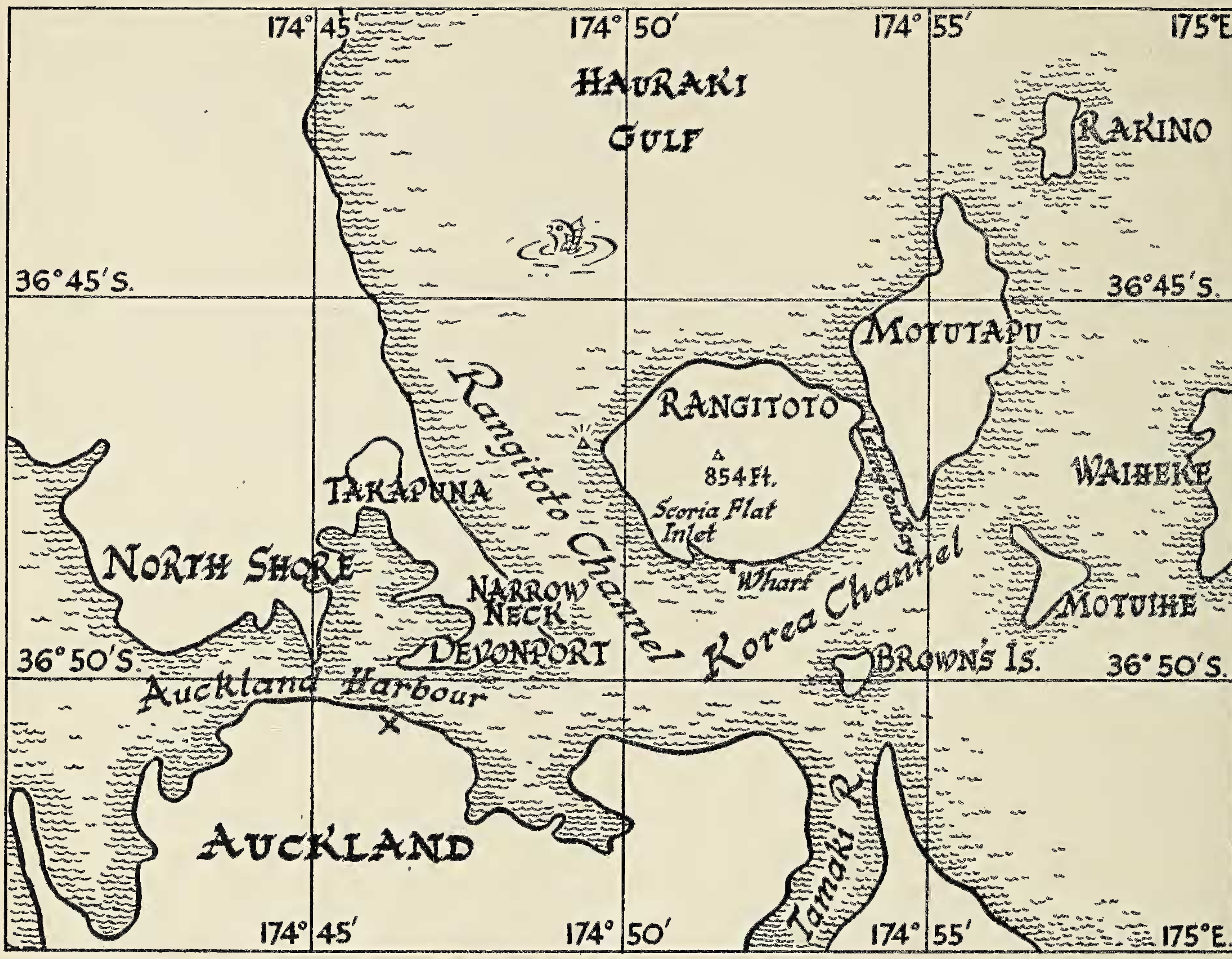


FIG. 1. Locality map of Rangitoto. Co-ordinates represent each 5 minutes of east longitude (top is north) and of south latitude. Scoria Flat Inlet shown west of Rangitoto Wharf. Position of Queen's Wharf indicated by ×. (N. Z. Defence Dept.)

mactic nature of rocky-shore communities and the seral nature of those of salt marshes.

In the present paper, the littoral is defined as the region between mean high water mark and mean low water mark of spring tides. Above this is a lower supralittoral region subject to occasional submergence, and below it is an upper sublittoral region subject to occasional exposure.

In the following account reference is made to certain tide levels. These are abbreviated as follows:

E.H.W.S.T. (extreme high water mark of spring tides)

M.H.W.S.T. (mean high water spring tides)

M.H.W.N.T. (mean high water neap tides)

M.L.W.N.T. (mean low water neap tides)

M.L.W.S.T. (mean low water spring tides)

E.L.W.S.T. (extreme low water spring tides)

The abundance or frequency of a species in a community is noted as: d (dominant), a (abundant), f (frequent), o (occasional), or r (rare).

CLIMAX COMMUNITIES OF ROCKY SHORES

As the local variant of the basic zonation suggested by Stephenson (1939), Chapman (1950) proposes four basic formations for the rocky shore climax of New Zealand. These, in order from top to bottom of the littoral, are the Littorinoid, Barnacle, Lower Littoral Mixed Algal, and Sublittoral Brown Kelp formations. It appears possible to build the pattern of distribution of species at Rangitoto into this framework.

Littorinoid Formation

This formation is that of the uppermost littoral and lower supralittoral. Its communities may reach upwards to the highest levels ever submerged.

There is one principal association on rock, although several fasciations occur where there is sediment. The patchy nature of the communities of the upper littoral differs from the usual "closed" nature of littoral communities on Rangitoto.

1. Melarhaphe-Lichina association

Melarhaphe oliveri d
Lichina pygmaea d
Bostrychia mixta f
Ralfsia sp. f
Placoma vesiculosa f

Lichina has a narrower vertical range than that of *Melarhaphe*, its upper limit being at M.H.W.S.T. Its lower limit is that of *Melarhaphe*, in the vicinity of M.H.W.N.T.

Several subordinate species occur, scattered within similar limits to those of *Lichina*, e.g., turfs of *Bostrychia mixta* are frequent, and there are also an encrusting *Ralfsia* sp. and small colonies of *Placoma vesiculosa*.

2. Caloglossa-Catenella fasciation

Caloglossa leprieurii d
Catenella nipae d
Bostrychia mixta f
Hildenbrandia prototypus o

This community occurs within the levels of the *Melarhaphe-Lichina* association, where there is some sediment. It is found particularly in crevices and other shaded places, where *Hildenbrandia prototypus* also takes part in the community. *Caloglossa* and *Catenella* are also found, together with *Rhizoclonium hookeri*, on mangrove pneumatophores (see "*Avicennia officinalis* consocies").

3. Myxophycean fasciations

Several Myxophycean communities are associated with varying degrees of sedimentation in the high tidal levels. These are dominated by one or more of the following species: *Calothrix scopulorum*, *Lyngbya semiplena*, *Phormidium ambiguum*, and *Oscillatoria nigroviridis*.

Barnacle Formation

The communities within this formation occupy the large mid-tidal portion of the littoral (M.H.W.N.T.–M.L.W.N.T.). The two principal associations are characterised by the co-dominance of the barnacle *Chamaesipho columna*.

4. Chamaesipho-Apophlaea association

Chamaesipho columna d
Apophlaea sinclairii d
Gelidium pusillum f

This association occupies the upper portion of the mid-tidal levels. The lower limits of both dominants, as individuals, lie well below the lower limit of the association, but *Apophlaea* is dominant only within the limits of the association. The vertical range of *Gelidium pusillum*, a scattered, turf-like species, lies across that of the association.

5. Chamaesipho-Saxostrea association (Fig. 2)

Chamaesipho columna d
Saxostrea glomerata d
Elminius plicatus f

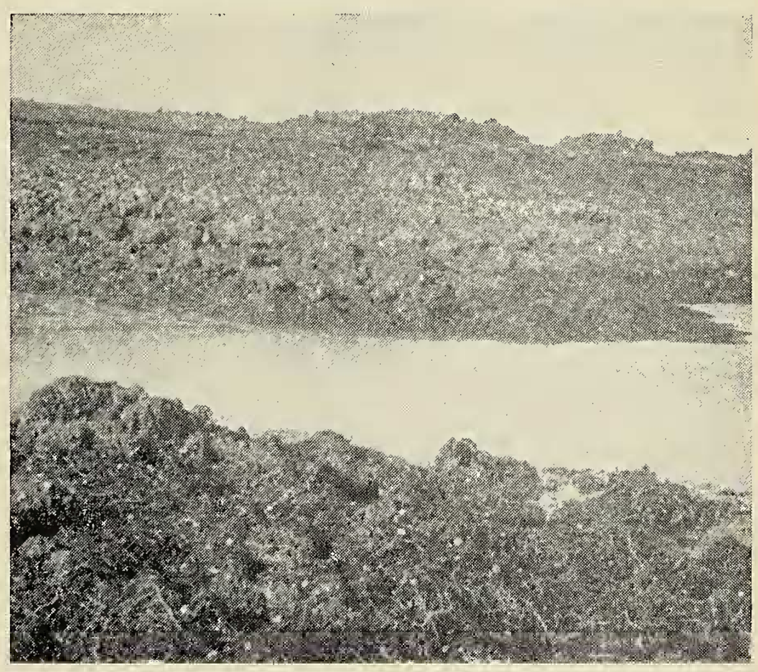


FIG. 2. Zonation on sloping scoria shore. *Chamaesipho-Saxostrea* association (white), *Corallina-Hormosira* association (grey), *Carpophyllum-Ecklonia* association (dark; bottom of slope and foreground).

Scytothamnus australis f
Apophlaea sinclairii f
Hormosira banksii o

This is the characteristic mid-tidal community of rocky shores on Rangitoto. The upper limit of this association coincides with the lower limit of the preceding association. The relative proportions of the two dominants vary with the environment. Thus, certain environmental conditions, which may differ for the two organisms, appear to be required for the optimum expression of each. As a result, in the extreme case, two consociations may be recognised.

Elminius plicatus, *Apophlaea sinclairii*, and *Scytothamnus australis* are scattered through the association. It is probable that the importance of *Apophlaea* above the upper limit of *Saxostrea* may be related to an absence of competition. *Scytothamnus* assumes local dominance in more exposed localities.

With an increase in physical exposure, *Chamaesipho brunnea* enters the association, to the extent of dominance. Its upper limit is above that of *C. columna*.

6. **Hormosira banksii consociation**
Hormosira banksii d
Scytothamnus australis f
Corallina officinalis f
Vermilia carinifera o
Microdictyon sp. o

The *Hormosira* community, classed under the mid-tidal formation, occupies approximately the same limits as the *Chamaesipho-Saxostrea* association of less protected shores. This plant, which is associated with physical shelter, may form a consociation on flat or broken surfaces. The community is very characteristic of scoria shores.

Vermilia carinifera may completely occupy such special substrates as isolated rocks and steep surfaces (Fig. 3).

7. **Elminius-Modiolus fasciation**
Elminius modestus d
Modiolus neozelanicus d
Gelidium pusillum o
Caloglossa leprieurii o
Scytothamnus australis o

This mid-tidal community occurs on the special substratum provided by wharves.

8. **Enteromorpha bulbosa-Monostroma crepidinum aspect**

A chlorophycean community occurs in the upper part of the levels of the formation between June and January. It is associated with physical shelter, but has no apparent relation to fresh-water drainage.

Lower Littoral Mixed Algal Formation

This formation occupies that part of the littoral which lies roughly between M.L.W.N.T. and M.L.W.S.T. It is noteworthy for the fact that all the dominants in the various communities are plants. A considerable variation in species composition is partly associated with changes in physical exposure. A basic association may, however, be recognised.

9. **Corallina-Hormosira association** (Fig. 2)
Corallina officinalis d
Hormosira banksii d
Codium adhaerens a
Colpomenia sinuosa a
Elminius modestus a
Cystophora torulosa a
Xiphophora chondrophylla var. *minus* a
Aeodes nitidissima a
Splachnidium rugosum f

Hormosira banksii exhibits a much-reduced thallus form as compared with the *Hormosira* plants from the upper part of its range. This appears to be associated with relative tolerance of water loss (see page 44).

Several important subordinate species appear to have ecological requirements fairly similar to those of the dominants. These are *Codium adhaerens*, *Splachnidium rugosum* (seasonal), and *Colpomenia sinuosa* (seasonal). *Elminius modestus* covers many pebbles and stones down to M.L.W.S.T.

FIG. 3. Zonation on sea wall (steep, solid surface). From top: *Saxostrea glomerata*, *Vermilia carinifera*, *Codium adhaerens*.

Much variation is produced within the levels of the association by the dominance of subordinate species under special conditions. *Codium adhaerens* flourishes on steep slopes (Fig. 3) and in shade, while the seasonal *Splachnidium rugosum* dominates on some fairly exposed slopes and boulders. *Cystophora torulosa* and *Xiphophora chondrophylla* var. *minus* occur at the junction of the *Corallina-Hormosira* and brown kelp communities in fairly exposed localities, and exhibit dominance with moderate and strong exposure, respectively. *Aeodes nitidissima* assumes seasonal local dominance at similar levels in more sheltered areas.

Sublittoral Brown Kelp Formation

This formation is represented by a very consistent association, which forms the kelp belt that encircles the island.

10. **Carpophyllum-Ecklonia association** (Fig. 2)

Ecklonia radiata var. *richardiana* d
Carpophyllum maschalocarpum d
C. flexuosum a
C. plumosum a
Pterocladia lucida f
P. capillacea f
Melanthalia abscissa f
Sargassum sinclairii o

Carpophyllum maschalocarpum, the principal *Carpophyllum* species, is generally present in larger proportions than *Ecklonia*. In addition, *Carpophyllum flexuosum* occurs with shelter and *C. plumosum* with exposure. *Sargassum sinclarii* is scattered within the association in sheltered places. Prominent subordinates in exposed areas are *Pterocladia lucida*, *P. capillacea*, and *Melanthalia abscissa*.

11. **Mytilus canaliculus-Tunicate fasciation**

This community occurs on vertical and shaded surfaces, which are unsuitable for the general establishment of the large phaeophyceans. Scattered specimens of *Ecklonia* and *Tethya fissurata* occur in the community.

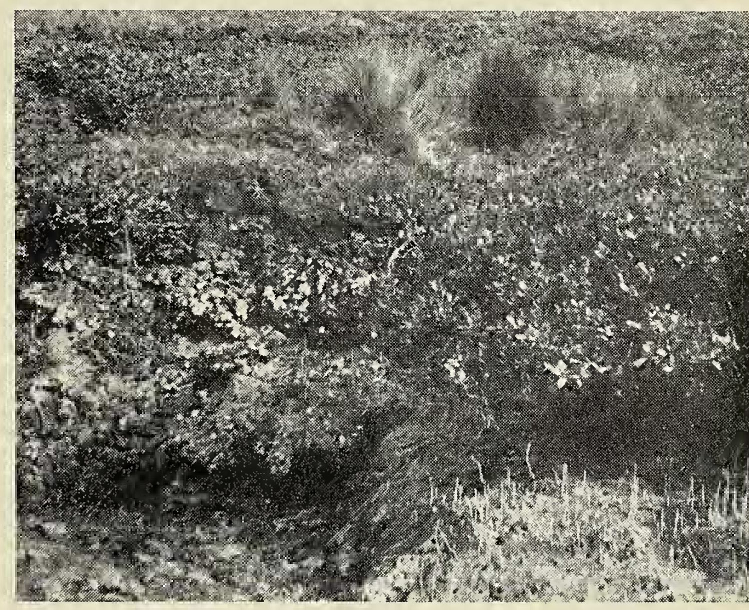


FIG. 4. Communities of Scoria Flat Inlet. *Salicornia-Stipa* associes (above), *Avicennia officinalis* consocies (showing pneumatophores), *Saxostrea glomerata* on vertical rock surfaces, and *Hormosira banksii* where there is sediment.

SERAL COMMUNITIES (Fig. 4)

The maximum development of seral communities takes place on sedimentary substrata in sheltered places. There is a zonation of several communities, each dominated by angiosperms. In each case, aggradation, characteristic of seral communities, occurs.

1. **Salicornia-Stipa associes**

Salicornia australis d
Stipa teretifolia d
Rhizoclonium hookeri f

Melarhaphe oliveri f
Suaeda maritima o
Triglochin striata var. *filifolium* r

This is principally a community of about M.H.W.S.T. In the shelter of the dominant angiosperms is a *Rhizoclonium hookeri* socies.

2. **Avicennia officinalis consocies**

This is a mid-tidal community. Although the vertical range within which mangrove seedlings will develop is narrow, a mature plant occupies a wide vertical range by virtue of its size. A community of *Rhizoclonium hookeri*, *Catenella nipae*, *Caloglossa leprieurii*, and sediment-fixing Myxophyceae occurs on the pneumatophores. In some areas, *Hormosira banksii* is attached to the pneumatophores, and to scoria where this is present. *Gracilaria secundata* f. *pseudoflagellifera* appears to be free-living on the surface of the mud.

3. **Zostera nana consocies**

This is the community of the lowest littoral and the upper sublittoral.

LEVELLING SURVEY

A numerical account of distribution was provided by means of a levelling survey. The species were treated individually because of the wide variety of vertical and horizontal ranges which produces the observed complexity of community groupings.

The upper and lower limits of the intertidal organisms were determined as relative to tide levels, both for the elucidation of causal factors and for correlation with similar work elsewhere. There being no bench marks on the island, all levellings were referred to marks established above E.H.W.S.T., these marks in turn being tied to E.L.W.S.T. as determined for the island (see "Tidal Factors"). The levels given below are based on E.L.W.S.T. as 0.00 feet.

Relation of Communities to Levelling (Figs. 5, 6)

The levels for an apparently normal zonation confirm the observed communities. There is a definite tendency for the majority of the upper and lower limits of species to occur in the vicinity of the apparent limits of formations and communities.

It is also possible to postulate critical levels at which significant changes in species composition occur. Five such levels were recognised on Rangitoto. The lowest critical level on the shore was placed at 1.50 feet, being the average of the seven upper limits and eight lower limits of species which were located between the levels 1.00 feet and 2.00 feet above E.L.W.S.T. Others were placed at 3.75 feet (five upper and three lower limits between 3.50 feet and 4.00 feet); at 8.00 feet (five upper and four lower limits between 7.50 feet and 8.50 feet); at 9.30 feet (seven upper and five lower limits between 9.00 feet and 9.75 feet); and at 11.00 feet (nine upper and three lower limits between 10.50 feet and 11.50 feet).

The numerical basis of these levels (to the nearest 0.5 foot) is shown in Figure 6. The principal levels of change in species composition are clearly in the vicinity of 1.5, 3.5, 9.5, and 11.0 feet.

FACTORS INVOLVED

Tidal Factors

Tidal Information. The tides at Auckland are of the normal semidiurnal type, with a diurnal inequality. Tidal measurements are made at Queen's Wharf by the Auckland Harbour Board's tide instrument. The zero for these measurements is E.L.W.S.T., taken as 3 feet above the Auckland Dock Sill. The Admiralty Datum, upon which the tidal data in the New Zealand Nautical Almanac are based, is 3.5 feet above the Dock Sill.

Tidal Behaviour at Rangitoto. Since it was intended to use the tide charts prepared by the Auckland tide machine in the calculation of submergence and emergence, and also because the correlation of littoral levelling with similar work elsewhere had of necessity to be through tide levels, a determination of

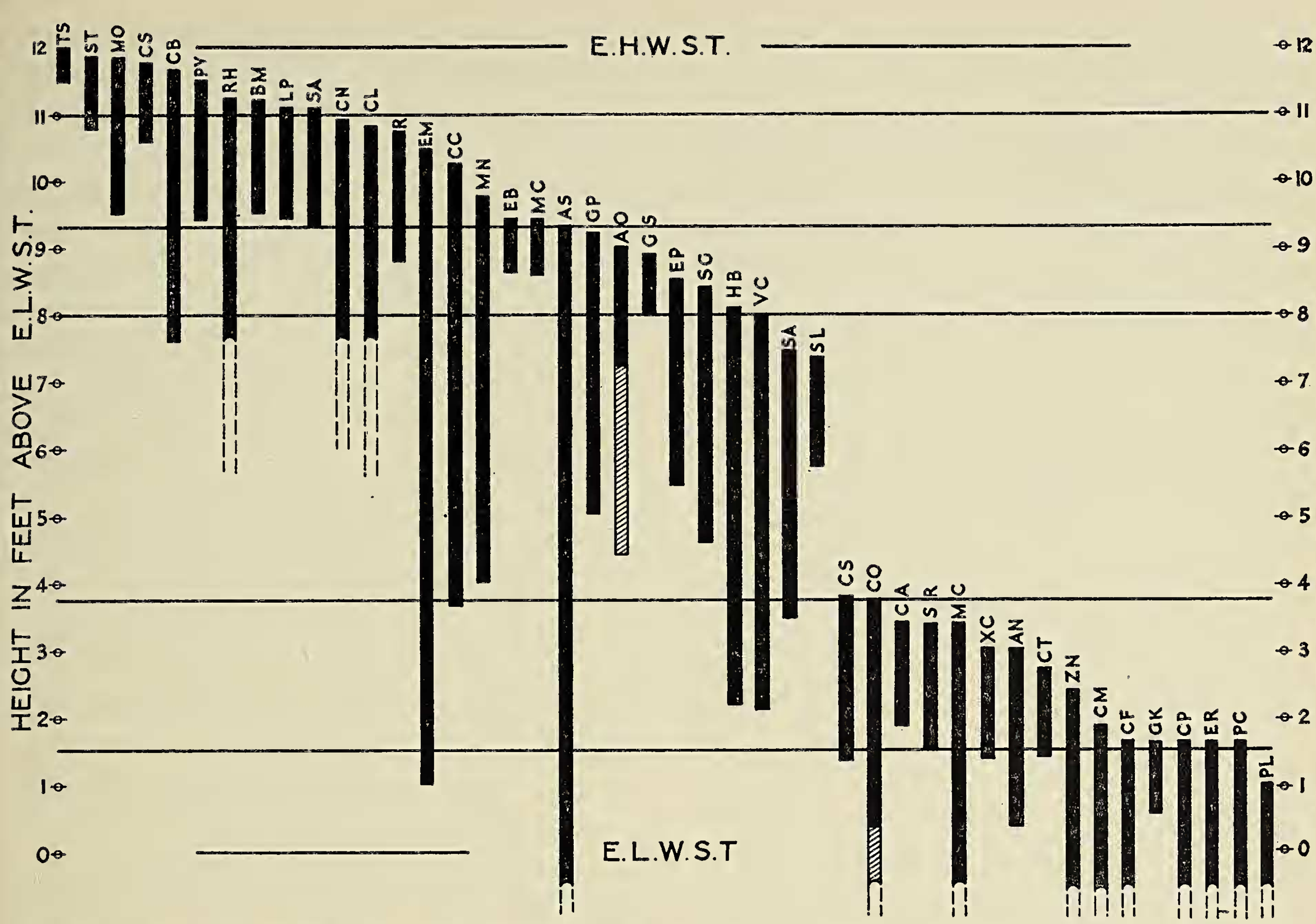


FIG. 5. Vertical ranges of important organisms. Significance of key letters in figure (reading from left to right):

TS Triglochin striatum
ST Stipa teretifolia
MO Melarhaphe oliveri
CS Calothrix scopulorum
CB Chamaesipho brunnea
PV Placoma vesiculosa
RH Rhizoclonium hookeri
BM Bostrychia mixta
LP Lichina pygmaea
SA Salicornia australis
CN Catenella nipae
CL Caloglossa leprieurii
R Ralfsia sp.
EM Elminius modestus
CC Chamaesipho columna
MN Modiolus neozelanicus
EB Enteromorpha bulbosa
MC Monostroma crepidinum
AS Apophlaea sinclairii
GP Gelidium pusillum
AO Avicennia officinalis
GS Gracilaria secundata
EP Elminius plicatus
SG Saxostrea glomerata
HB Hormosira banksii
VC Vermilia carinifera
SA Scytothamnus australis
SL Scytosiphon lomentaria
CS Colpomenia sinuosa
CO Corallina officinalis
CA Codium adhaerens
SR Splachnidium rugosum
MC Mytilus canaliculus
XC Xiphophora chondrophylla
AN Aeodes nitidissima
CT Cystophora torulosa
ZN Zostera nana
CM Carpophyllum maschalocarpum
CF Carpophyllum flexuosum
GK Glossophora kunthii
CP Carpophyllum plumosum
ER Ecklonia radiata
PC Pterocladia capillacea
PL Pterocladia lucida

tidal behaviour relative to that at Auckland was undertaken at Rangitoto.

When possible, days of dead calm were chosen for tidal readings. The principal station for tidal measurements was the bridge at Scoria Flat Inlet, on the southwest shore of the island. The times, and heights relative to the centre point of the bridge deck, of high water under the bridge were accurately determined on a number of days. No low-water readings were possible, inasmuch as the Inlet dries out. A reasonable correlation with the times and heights of the same tides at Auckland was obtained. The vertical distance of E.H.W.S.T. below the bridge deck was determined, and E.L.W.S.T. placed 12.0 feet lower, as at Auckland. This was justified by observations of the tidal ranges elsewhere on the island. For this purpose tide poles were established and the times and heights of high and low water accurately determined. The times of high and low water were almost identical with those at Auckland, but there seems to be a slight local variation in the tide range at each place as compared with that at Auckland. Full-tide curves made at Rangitoto Wharf (south coast) show no irregularities.

For the comparison of the levellings at the various places with the levellings at Scoria Flat, E.L.W.S.T. was approximately determined on the basis of the tide readings made at each place, equality being assumed between the Auckland and the local tides.

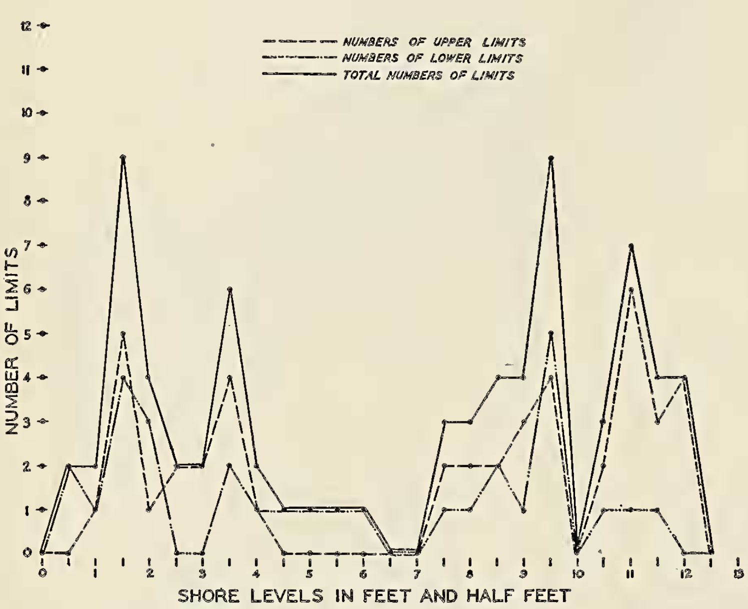


FIG. 6. Distribution on the shore of upper and lower limits of organisms. Total numbers of limits (upper plus lower) for each level also shown.

Principal Tide Levels. The limits 0.00 feet and 12.00 feet (above AHB Datum), representing E.L.W.S.T. and E.H.W.S.T., are never normally exceeded by tidal fall or rise.

Certain levels for Queen's Wharf for 1947 were calculated from the Nautical Almanac predictions (in each case the calculated level is followed by the average of the actual recorded tides at Queen's Wharf for the 3 years 1945–1947, by courtesy of Miss U. V. Dellow). These levels are: E.H.W.S.T., 11.90 feet (11.95 feet); M.H.W.S.T., 11.01 feet (11.41 feet); M.H.W.N.T., 9.22 feet (9.28 feet); M.L.W.N.T., 3.31 feet (3.29 feet); M.L.W.S.T., 1.36 feet (1.12 feet); E.L.W.S.T., 0.60 foot (0.60 foot).

The lowest high water recorded is extreme (low) high water of neap tides (E.(L.)H.W.N.T.), and the highest low water is extreme (high) low water of neap tides (E.(H.)L.W.N.T.). All levels between these (8.40 feet [8.88 feet] and 4.00 feet [3.96 feet], respectively) are subjected to alternating submergence and emergence twice in every 24 hours. For all levels above E.(L.)H.W.N.T. there is, therefore, a varying amount of continuous emergence; and similarly, for all levels below E.(H.)L.W.N.T., a varying amount of continuous submergence.

The correlation of tidal information with critical levels may be given as:

The critical level 1.5 feet is just above M.L.W.S.T.

The critical level 11.0 feet is just below M.H.W.S.T.

The critical level 3.75 feet lies between M.L.W.N.T. and E.(H.)L.W.N.T.

The critical level 9.3 feet is approximately M.H.W.N.T.

The critical level 8.0 feet is below E.(L.)H.W.N.T.

Significance of Tide Levels. Some of these levels appear to represent thresholds. For example, E.(L.)H.W.N.T. is the highest level of regular, semidiurnal, alternating submergence and emergence, while E.(H.)L.W.N.T. is the lowest level regularly uncovered by the tide. To determine the significance of such levels, the tidal factor was analysed with respect to submergence-emergence relations and to continuous emergence and submergence.

The submergence-emergence behaviour of the tides at Auckland was determined from the tide charts prepared by the instrument at Queen's Wharf. These charts are graphs of sea level against time. Calculations were made of the relative submergence and emergence of the different levels between the extreme limits of inundation, expressed in terms of the percentage of the total time considered during which each 1-foot level was not submerged. This was done for a tidal period of 360 hours (spring to spring) (Fig. 7A). A better average is obtained over a lunar month, or better, a lunar year (Fig. 7B).

The probable significance of relative sub-

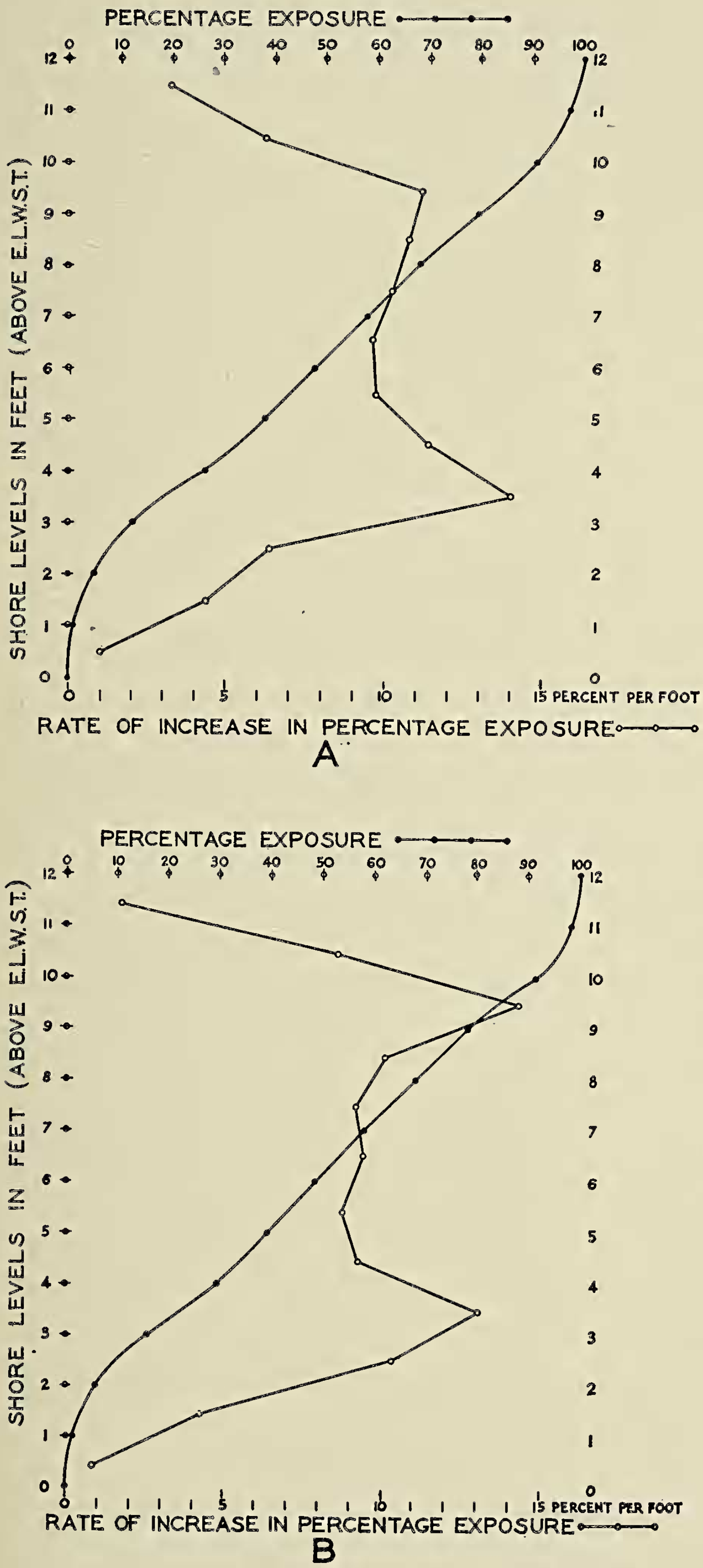


FIG. 7. Percentage emergence ("percentage exposure") for each foot between E.L.W.S.T. and E.H.W.S.T. A, for one tidal period (360 hours), Jan., 1947; B, for one lunar year (1945) (A. E. Beveridge). Rate of increase in percentage emergence ("percentage exposure") also shown in each case.

mergence and emergence lies in the rate of increase of percentage emergence with height on the littoral (Fig. 7). This rate of increase rises to two peaks, occurring between 3.0 feet and 4.0 feet and between 9.0 feet and 10.0 feet. These sharp changes in the rate of increase might be the basis of thresholds in the vicinity of M.L.W.N.T. (3.31 feet) and of M.H.W.N.T. (9.22 feet).

Calculations were made (from the Nautical Almanac predictions) of the periods of continuous emergence undergone by each level above E.(L.)H.W.N.T. in 1947, and of the periods of continuous submergence undergone by each level below E.(H.)L.W.N.T.

The maximum period appears to be important in each case. In the case of emergence, it is 1 day at 8.5 feet (through missing a single tide). It then rises fairly steadily to 9 days at 10.0 feet. There is a fairly sharp rise to 23 days at 10.5 feet and to 43 days at 11.0 feet. A great increase in the maximum period of emergence then occurs, the time being 132 days at 11.5 feet. Above M.H.W.S.T., a condition of permanent emergence is swiftly attained. Fairly similar behaviour is associated with the periods of continuous submergence. Here a fairly steady rise to 25 days at 1.5 feet is followed by a sharp rise to 131 days at 1.0 foot. The 0.5 foot level is permanently submerged.

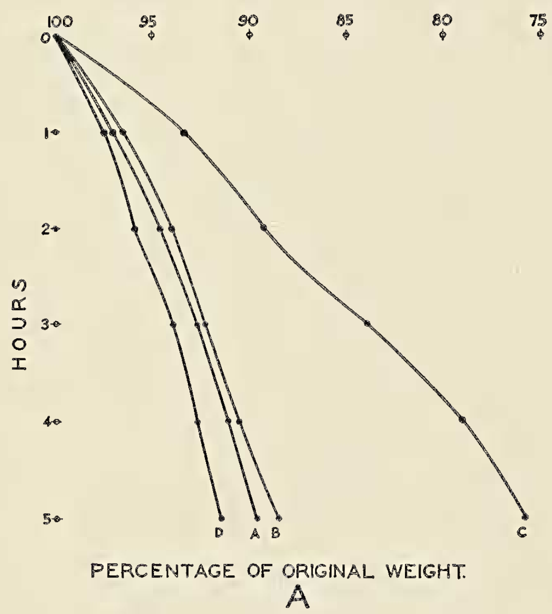
The important point would appear to be the meaning given to the mean limits of spring tides (defined under "Terminology" as the limits of the littoral) by the great rises in the maximum periods of continuous emergence and submergence at M.H.W.S.T. and M.L.W.S.T., respectively. Here again the levels appear to be thresholds.

The relatively large increase in maximum continuous emergence between 10.0 feet and 11.0 feet may control the upper limits of *Chamaesipho columna* (10.3 feet) and *Elminius modestus* (10.5 feet).

Behaviour of Hormosira banksii. In each of the above cases, it would seem that phenomena associated with tidal inundation provide physiological limits to the vertical distribution of littoral species. Each change in environmental conditions is a barrier which cannot be surmounted by certain species, either in establishment as young plants or animals, or in development.

Reaction to the causal factors is shown in one way by *Hormosira banksii*. This alga plays a prominent part in the littoral ecology of Rangitoto because its vertical range is from M.L.W.S.T. to E.(L.)H.W.N.T. The young plant, or "button," is found throughout this range and up to 1 foot above the upper limit.

Mature plants show considerable variability. The size of the plants, with regard to the size of the receptacles (and, to a lesser degree, to the number thereof), is proportional to their height above E.L.W.S.T. (The average diameter of the receptacles ranged from 1.50 centimetres in plants near the upper limit of the species to 0.75 centimetre in plants near the lower limit.) Further, the thickness of the wall of the receptacle was found to be inversely proportional to the diameter. (The average thickness of the walls ranged from 0.11 centimetre in plants near the upper limit of the species to 0.14 centimetre in plants near the lower limit.) Finally, the rate of water loss from plants during emergence was found to be inversely proportional to their height on the shore (Fig. 8). On the basis of these measurements, the rate of water loss is, therefore, inversely proportional to the volume of the water-filled, hollow interiors of the receptacles. In support of this, determinations of the above quantities were also made with samples of a special, large form of *Hormosira* (D in Fig. 8), which is found back from the shore in those low scoria areas where tidal seepage occurs. The receptacles of these plants were found to have an average diameter of 1.70 centimetres and an average wall-thickness of 0.10 centimetre, and their rate of water loss was the lowest recorded.



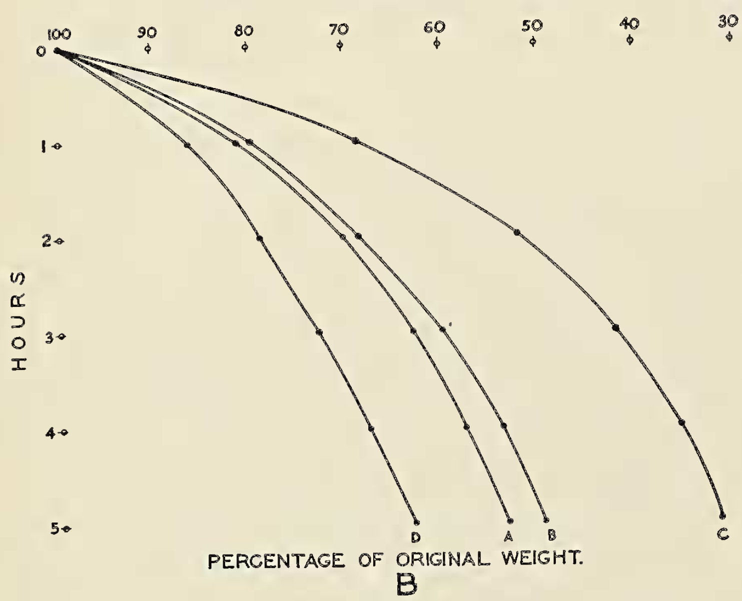


FIG. 8. Loss of weight of *Hormosira banksii* thalli during emergence ("exposure"). Mean percentage loss of weight per hour (under identical conditions) of: A, numbers of plants of *Hormosira banksii* from top of range; B, main *Hormosira* consociation; C, *Corallina-Hormosira* association; and D, of special form (see text). 8A, in laboratory; 8B, in sunlight.

It seems possible, therefore, that the relatively large vertical range of *Hormosira banksii* depends on a considerable tolerance of differences in submergence-emergence relations in the "button" stage, together with morphological variation in the adult in relation to the degree of desiccation undergone at different levels.

Other Factors

In the foregoing section, the fundamental nature of zonation as a function of the tidal factors has been discussed. The final pattern of distribution may be considered as the product of the reaction of the basic vertical zonation with a set of variables.

The object of the work classed under this section was the determination of these variables, partly from detectable variations in the vertical levelling and partly in more empirical ways.

The factors sought may be classified roughly into two groups: the modifying factors, evidenced by variations in vertical distribution; and the presence-or-absence factors, as manifested by differences in transect composition.

Modifying Factors. Most of the observed variations in vertical distribution took the form of raised upper limits. There were few cases of lowering of lower limits. The general basis of the factors inducing the former may be the prevention of normal desiccation, and of the latter, the lessening of normal submergence. The upper limit of *Hormosira banksii* is raised by as much as 1.0 foot by prevention of run-off on fairly flat scoria shores and in mangrove swamps. Similarly, seepage induced by the pervious nature of the scoria substratum results in the occurrence of *Zostera nana*, *Aeodes nitidissima*, the kelps, and species of *Pterocladia* in the lower littoral at much higher levels than those determined by the tidal factors.

At exposed points, the upper limits of some species at the upper boundary of the littoral may be raised to considerable heights through the influence of spray, while aeration may lower the lower limits of some species at the lower boundary of the littoral. *Melarhaphe oliveri*, whose normal upper limit is E.H.W.S.T., is found on the northern coasts on top of the cliffs, 10.0 feet or more above theoretical E.H.W.S.T. In exposed places, *Chamaesipho columna* may be found dominant down to E.L.W.S.T., more than 2 feet below its lower limit, on less exposed shores. This may be due to wave-induced aeration or to increased light because of the clearer water of the outer shores.

The micro-climates, provided by the topography of the scoria or by actual vegetation, present another case of the raising of upper limits by the reduction of exposure-induced desiccation. Within clefts in the upper littoral, where the relative humidity was determined by rough wet-and-dry bulb tests to be about 25 per cent higher than in the open, the upper limits of *Catenella nipae* and *Caloglossa leprieurii* are raised by 0.7 foot. Under *Hormosira banksii* thalli, similar tests show the humidity to be about 30 per cent higher than in the open. In the *Hormosira* consociation, the subordinate *Corallina officinalis* occurs up to 3.0 feet above its normal upper limit, and *Microdictyon* sp. nearly as much.

In other cases, direct protection from insolation appears responsible for raising the upper limits of species, e.g., *Codium adhaerens* (raised 1.5 feet) and *Ecklonia radiata* var. *richardiana* (0.75 foot).

Presence-or-absence Factors. Of the factors controlling the presence or absence of species at one point, the one best exhibited at Rangitoto is relative physical exposure. The geography of the island provides a wide range of conditions. It would appear that physical exposure inhibits the establishment of some species, while sheltered conditions, and especially the encouragement of sedimentation, act against other species.

Xiphophora chondrophylla var. *minus*, *Carpophyllum plumosum*, *Pterocladia lucida*, *P. capillacea*, *Glossophora kunthii*, and *Chamaesipho brunnea* occur only under conditions of exposure, while *Hormosira banksii* occurs only in shelter. *Cystophora torulosa*, *Scytothamnus australis*, and *Splachnidium rugosum* are dominant only in exposed places. Conversely, *Saxostrea glomerata* thins out with exposure. Most of the other dominants, however, appear indifferent to the degree of physical exposure. *Corallina officinalis* is reduced to its basal portion by exposure.

The nature of the substratum affects the presence or absence of species. The sedimentation induced by shelter results in fasciations and seral communities. In the case of the predominant rocky shores, the variable nature of the basalt is often the indirect basis of other environmental variations. The scoria shores, the broken surfaces of which provide pockets of shelter, are likely to show a mosaic of climax and seral communities.

General texture may be involved (Fig. 3). An unbroken surface favours *Saxostrea glomerata*. At lower levels, an unbroken surface favours *Codium adhaerens* and a broken one the *Corallina-Hormosira* association. The *Carpophyllum-Ecklonia* association requires a solid substrate for the attachment of the large dominants. Boulders on an exposed shore appear to favour a zonation of *Scytothamnus australis*, *Splachnidium rugosum*, and *Glossophora kunthii*.

Physical exposure appears to be reduced by a flat shore so that a habitat, such as the top of a lava flow, results in the development of the *Hormosira banksii* consociation, while *Saxostrea glomerata* occurs on slopes. Further, *Codium adhaerens* tends to dominate on vertical surfaces (Fig. 3), while *Corallina officinalis* and *Hormosira banksii* are best developed on flatter shores. Again, vertical surfaces in the upper sublittoral bear *Mytilus canaliculus*, tunicates, and some *Ecklonia* in place of the usual *Carpophyllum-Ecklonia* association.

Finally, differences in shade tolerance produce some variations. *Carpophyllum maschalocarpum* is reduced in shade, while *Ecklonia* is more tolerant. In the shade of the kelps, *Corallina officinalis* is reduced to its basal filaments, while *Aeodes nitidissima* is eliminated. *Codium adhaerens* is favoured by shade to the extent of frequent dominance in the levels of the *Corallina-Hormosira* association on the southern sides of rocks. It is probable that the discoloration of sheltered waters by sediment in suspension, with subsequent light reduction, operates in excluding at least some of the species associated with physical exposure.

Tidally Controlled Variations. It must be noted that not only seasonal climatic conditions but also seasonal variations in tidal behaviour may be responsible for the fluctuations of some species. Thus the occurrence in the autumn of the maximum periods of continuous submergence of the lower littoral levels for the year may have been responsible for the establishment of *Colpomenia sinuosa* and the disappearance of *Splachnidium rugosum* in that season. Similarly, the spring maximum of the *Enteromorpha bulbosa–Monostroma crepidinum* aspect might be associated with the fact that the maximum periods for the year of continuous emergence in the upper littoral occurred at that time.

SUMMARY

An attempt has been made to classify the communities of inter-tidal plants and animals at Rangitoto Island. The climax communities appear to fit into the general, basic, rocky-shore zonation for New Zealand.

The causal factors in vertical zonation at Rangitoto, namely, those determining the upper and lower limits of species, have been related to tidal phenomena. Attention has been given to the behaviour relative to tide levels of *Hormosira banksii*. The variables, which produce variations in the vertical limits of species and in species composition, have been sought in environmental factors other than tidal.

REFERENCES

BEVERIDGE, A. E., and V. J. CHAPMAN. 1950. The zonation of marine algae at Piha, New Zealand, in relation to the tidal factor. (Studies in inter-tidal zonation 2.) *Pacific Sci.* 4 (3): 188–201.

CHAPMAN, V. J. 1946. Marine algal ecology. *Bot. Rev.* 12 (10): 628–672.

——— 1950. The marine algal communities of Stanmore Bay, New Zealand. (Studies in inter-tidal zonation 1.) *Pacific Sci.* 4 (1): 63–68.

STEPHENSON, T. A. 1939. The constitution of the inter-tidal fauna and flora of South Africa. Part I. *Linn. Soc. London, Jour., Zool.* 40: 487–536.